

12

Oligochaeta: Megascolecidae and Other Earthworms from Western North America

WILLIAM M. FENDER

DOROTHY McKEY-FENDER

The terrestrial earthworm fauna of the western United States is composed primarily of two groups, the native species and the introduced Lumbricidae (Fender 1984). The native earthworms are of the family Megascolecidae in the broad sense (Acanthodrilidae and Octochaetidae *sensu*, Gates 1959), and include several genera. The bulk of these species were traditionally placed in *Plutellus* Perrier but were removed to *Argilophilus* Eisen, 1893 (Jamieson 1972, Gates 1977b). Two other genera, *Arctiostrotus* (McKey-Fender and Fender 1982) and *Kincaidodrilus* (McKey-Fender 1982), have recently been described to contain several species that did not fit well into *Argilophilus*. Many new species are being described in a revision of the argilophiline earthworms which is presently being compiled by us. We consider all of these species to belong to a single tribe, herein called the Argilophilini. Brief descriptions of several new genera and a more detailed taxonomic discussion are given later in this chapter. The second group, the adventive Lumbricidae, now predominate in most agricultural and urban areas, whereas the native Megascolecidae predominate where native vegetation is still dominant.

In addition to the two groups above, there are a few species of exotic genera of the Megascolecidae (*Pheretima* and its segregates, *Microscolex* and *Dichogaster*) and Ocnerodrilidae (*Eukerria* and *Ocnerodrilus*). These taxa are not especially abundant anywhere in the western United States, but are more commonly encountered in southern areas.

Range

The Argilophilini occur in a narrow strip of Pacific coastal North America. In British Columbia they appear to be limited to the coastal islands, a single species (*Arctiostrotus perrieri*) having been described from the Queen Charlotte Islands and that species and two others having been collected from Vancouver Island. In Washington, they are present along the entire coast, but in the Puget lowlands and Cascade Range only south of the Puget Sound. Two species are found in the Columbia Gorge in Washington. *Driloleirus americanus* is found in the area around Pullman, Washington, and Moscow, Idaho, and in the hills west of Ellensburg, Washington, but is not known from the arid land between. Several species of *Arctiostrotus* are now known from central Idaho. In Oregon, the argilophiline worms are present in great diversity west of the Cascade Range but eastward have been found only in the Dalles area (two species) and in the Ochoco Mountains (two species?) and Blue Mountains (one species). The apparent paucity of species in that area could be a collecting artifact, but most of central and eastern Oregon is too dry for earthworms, and pumice soils inimical to earthworms blanket most of the east slope of the Cascade Range. Southward, argilophiline worms have been found in northern and central California in the mountains and along the coast (although not on the dry floor of the Sacramento Valley) as far south as Santa Cruz and Tulare counties. The species diversity drops rapidly southward, only two species, *Argilophilus sierrae* and *A. papillifer*, having been collected south of San Francisco Bay.

No argilophiline worms are known south of Tulare County in the United States, but a single specimen, described as *Argilophilus hyalinus* Eisen, 1900, was collected from Guatemala. This specimen, in poor shape to begin with, was lost in the San Francisco earthquake and fire of 1906, but of its general affinities there can be little doubt. No native earthworm species are known from western North America outside Washington, Idaho, Oregon, California, and the islands of coastal British Columbia. The nearest relatives of the Argilophilini are to be found in southeast Asia (Gates 1972), and although there are no congeners in the two areas, some of the Asian "*Plutellus*" species could possibly fit within the Argilophilini.

Anatomy and Function

Peregrine Lumbricidae can usually be identified to species simply by external features, but in the Megascolecidae, specimens must be dissected to identify the genus, and identification to species requires an intimate knowledge of earthworm anatomy.

The argilophiline worms are cylindrical in cross section except in the area of the clitellum; the posterior end is never flattened as in the Lumbrici-

cidae, but is usually expanded to form a "caudal bulb." The ambulatory setae are in eight regular rows and are generally not closely paired. The worms are, with few exceptions, unpigmented and the coelomic fluid is a milky white due to the presence of abundant coelomocytes. They often have a marbled appearance posteriorly where the milky coelomic fluid and the dark chloragogen alternatively show through the thin body wall.

The clitellum is closely associated with both the female and male pores, covering at least segments 13–18, and may extend onto segment 12 anteriorly and/or to segment 22 posteriorly (*Driloleirus* spp.), whereas in the Lumbricidae the clitellum is always posterior to 18. The clitellum may be a complete ring, or may be divided ventrally. Round, oval, or transversely elongate suckerlike genital markings are present on the anterior ventral surface of the body (not just in the clitellum), usually intersegmentally. These aid in attachment during copulation, since no slime tube is formed by these worms. Tubercula pubertatis and genital tumescences such as are found in the Lumbricidae are absent in the Megascolecidae. The male pores are a single pair on segment 18 (15 in the Lumbricidae) and are in glandular porophores in line with *A* and *B* setal rows. They are combined with the pores of cylindrical "prostates" and are associated with modified "penial" setae, which are generally longer and more slender than the ambulatory setae and lack the nodule of the latter. These setae apparently act as an intromittent organ, entering the spermathecal duct and guiding the passage of sperm; similar penial setae and prostates are present in *Diplocardia* but in the segments adjacent to that bearing the male pores. Female pores are on 14. Spermathecal pores are in line with setal row *B* and are usually in or near intersegments 7/8 and 8/9, although some species possess only one pair in 7/8 or 8/9 and others have as many as five pairs, the most posterior being in 8/9. In some genera these pores are nearly invisible. The corresponding spermathecae are in the segment posterior to the intersegment and typically have a thick duct containing or bearing a lateral diverticulum in which the spermatozoa are stored, and a terminal ampulla. In one group of *Argilophilus* spp. the diverticulum has disappeared and spermatozoa are stored in the ampulla. Gonads and their funnels are as in the Lumbricidae; testes in *x* and *xi*, ovaries in *xiii*.† Ovaries are composed of numerous egg strings rather than a single egg string as in the Lumbricidae. Seminal vesicles are postseptal from 10/11 and 11/12 only (i.e., none are anteseptal). Ovisacs are postseptal on 13/14, and small ovisac-like rudiments are postseptal on 12/13. "Testis sacs" such as in *Lumbricus terrestris* are not found in the western natives, although a similar arrangement has arisen in *Arctiostrotus perrieri*, where the testes of *xi* have disappeared and those of *x* have become enclosed by the adherence of septa 9/10 and 10/11. While the oviducts pass from the ovifunnels directly to the wall in *xiv*, the

† We use the convention of referring to internal segmental locations by Roman numerals, external ones by Arabic numerals, and septa by two Arabic numerals separated by a slash.

sperm ducts travel backward just under the peritoneum to segment xviii, where they connect to the ental ends of the prostate ducts. The prostates are tubular and coiled or folded into a mass and are composed of two parts: the glandular ental portion, and a much shorter duct which is covered with shining circular muscle. The sperm ducts connect to the prostate at or very near the juncture of the duct and gland.

Gastrointestinal System

The alimentary canal is divided into a series of functional parts. This series is similar to that of *Diplocardia* and differs strongly from that in the Lumbricidae. Just inside the mouth is the pharynx, which contains a dorsal glandular pad, or tongue, which can be extruded from the mouth and aids in feeding, probably also providing the first digestive enzymes to be mixed with the food. The "saliva" of most Argilophilini has a definite flowery or spicy odor, characteristic of the species, and is perhaps involved in defense since it may be copiously produced in response to a mechanical stimulus. Behind the pharynx, of segment iv or iv-v, is a nonmuscular crop which serves for storage of food until it is processed by the muscular gizzard, which is in v, v and vi, vi, or vi and vii. Even though it may occupy more than one segment, the large muscular gizzard is a single structure, not double as in *Diplocardia*, and is derived from segment v. The gizzard of the Lumbricidae is in segment xvii and is not a homologous structure. In segments (ix)x-xiii(xvii) is a highly vascularized region of the esophagus which produces spherules of solid CaCO_3 . This region of the esophagus may be a simple tube (as in most species) or may have portions organized into distinct calciferous "glands" communicating with the lumen of the esophagus only by ducts (*Kincaidodrilus*), but it always has abundant blood-filled flaps, or lamellae, on its inner surface and it is from these flaps that the CaCO_3 is produced (compare to the calciferous gland of lumbricids and *Diplocardia*; Smith 1924). The floor of the calciferous esophageal region may be flat or with a single or double ridge (the "ventral esophageal typhlosole"). Between the calciferous region and the expanded intestine is a valvular constriction composed of one to three segments.

The intestine of the Argilophilini has four parts: pretyphlosolar (peristaltic) region, anterior typhlosolar (secretory) region, posterior typhlosolar (absorptive) region, and rectum. The peristaltic region extends from the intestinal origin (xvi-xix) to the typhlosole origin and may comprise 2-10 segments. As the name implies, this portion of the intestine is a mixing region with muscular (though thin) walls that in life are in constant motion. This region is in the same area and is homologous with the gizzard and crop of the Lumbricidae. The typhlosole begins in the region of xix-xxix, usually abruptly. Unlike the lumbricid typhlosole, which is an infolding of the entire intestine dorsum, the megascolecid typhlosole involves only the inner intestine wall and contains a vascular sinus. It may be variously bifur-

cate, forming a T- or Y-shaped or more complex structure (viewed in cross section), but it has none of the transverse grooves or flaps characteristic of many lumbricid typhlosoles. All argilophiline species have a typhlosole, but in a few species it is reduced to a vein in the intestine dorsum. In these cases it may be difficult or impossible to find the typhlosole in poorly preserved specimens (see note on preparation of specimens). The anterior typhlosolar region is nearly cylindrical, has relatively thick walls with a dense coating of brown or black chloragogen, and is secretory in function, as can be observed in anesthetized worms dissected in Ringer's solution. In *Drilo-chaera* the anterior intestine is covered by a pearly white layer of unknown function. Several (apparently unrelated) taxa possess ceca in this region of the intestine. The ceca appear to be secretory. Most species have a longitudinal groove midventral in the anterior typhlosolar intestine. This groove is flanked by ridges bearing long, dense cilia, which can be observed in living specimens to beat backward, while similar shorter cilia on the adjacent intestine wall beat toward the midventrum. The posterior typhlosolar region has a thinner wall and is more slender, but is tortuously arranged. It is this area that gives the "marbled" appearance (see above). The rectum is the final portion of the alimentary canal and may comprise the last 10–20 segments or so [i.e., the portion in the caudal bulb (see above)]. It lacks any trace of the typhlosole and may be empty or contain the rather dry pelletlike castings of this group. These firm castings are quite characteristic and probably contribute to the well-granulated character of the soil in some areas the worms inhabit.

Excretory System

Most Argilophilini have a single pair of nephridia in each segment starting with segment ii; there is always a set of nephridia which can be seen to derive from segment ii. However, only in *Arctiostrotus* are the nephridial funnels functional outside the rectal region. The remaining genera have small nonfunctional stalked mass of cells, except in the rectal area, where the funnels are large and functional. The nephridia are distinctly tubular in shape (i.e., without a thick glandular investment covering the tubules). In *Arctiostrotus*, the subterminal portion of the duct is expanded into a bladder. In all Argilophilini, the ducts enter the body wall at or near the site of the nephropore; in the Lumbricidae the nephridial ducts enter the body wall in *B* and pass subepidermally to the site of the pore. *Driloleirus* spp. are meronephric (i.e., having numerous nephridia in each segment). Most of the nephridia are blind entally, but the medianmost nephridia have the characteristic preseptal funnels of normal holonephridia, although these are nonfunctional mass of cells outside the rectal area.

There is a definite, though poorly developed tendency toward buccal enteronephry in the Argilophilini. This is the condition where the anterior nephridia empty into the buccal cavity rather than to the body surface.

Only in *Driloleirus americanus* has this reached the stage of an actual bladder emptying directly into the buccal cavity from the anterior nephridia, but in *Archistrotus* the anteriormost nephropores are associated with the ends of the prostomial grooves, allowing fluid to flow to the opening of the mouth along those grooves. We hypothesize that this has the effect of encouraging microbial growth within the intestine, by adding nitrogen to the otherwise nitrogen-poor food supply of these worms.

Circulatory System

The vascular system, as in the Lumbricidae, has a pulsing dorsal vessel which carries the blood forward, and a nonpulsing ventral vessel which distributes blood to the various tissues. These are connected by a series of commissures in the anterior. Anterior to segment x these commissures are noncontractile and attach to the dorsal vessel, the ventral vessel, and the parietes. In segments x–xii(xiii) are “lateroesophageal hearts.” These commissures are pulsing and have a large connection to the esophagus dorsum, a small connection to the dorsal vessel, and feed directly into the ventral vessel; lumbricid hearts connect only to the ventral and dorsal vessels. The ventral vessel in these segments is unbranched. These “hearts” have a series of valves that impart a beaded appearance, but the dorsal part is generally much longer than the others.

Nervous System

There are no subneural nor lateral neural vessels in the Argilophilini. Instead, two pairs of parietal trunks are present at about the level of the nephridia, and these appear to perform the same function of connecting the parietal circulation between the posterior segments.

Reproduction

The Pacific coast states are dominated by a maritime climate with mild, rainy winters and hot, dry summers and the native earthworms have developed a reproductive cycle that mirrors this fact. Nearly all species have a peak of cocoon production in the late winter and early spring months, and in most species this is followed by a summer-long estivation. Especially in *Argilophilus* spp. the sexual organs regress, and in *A. garloughi* they disappear entirely. Only those taxa that live in the moist coastal forests and in the High Cascades will maintain activity throughout the summer. Various Lumbricidae, notably *Aporrectodea trapezoides*, will stay active as long as the ground is sufficiently moist, so it is quite possible, by collecting late in the season, to collect nothing but Lumbricidae in areas that a month earlier would have been dominated by the native species. Activity resumes after

the ground becomes thoroughly moist in the fall, but the clitellum and other sexual structures will generally not regain full size until midwinter.

Parthenogenesis

To judge by morphological and ecological evidence, parthenogenesis is not nearly as common among the Argilophilini as has been suggested (Gates 1977b), but it does occur. *Arctiostrotus perrieri*, *Chetcodrilus umbellulariae*, and *Argilophilus sierrae* are all commonly, perhaps usually parthenogenetic. All three are widespread "weedy" species and can be found in fairly disturbed situations. Features that we use as indicators of parthenogenesis include consistent lack of mature sperm on funnels and in spermathecae of mature individuals, frequent aberrations of morphology and/or number of male sexual structures, extreme parasitism of the seminal vesicles and male segments, and lack of the genital papillae which function in copulation.

Habitats

Much of the ecological literature on earthworms, especially from the temperate zones, treats Lumbricidae only, and the other families, when they are recognized as existing at all, are considered to be on the way to being exterminated by the more aggressive Lumbricidae. There is some justification for this picture in the western United States, at least on the surface. If one looks for earthworms in lawns, gardens, fields, roadside ditches, irrigated areas, pastureland or grazed woodlots, coarse-textured soils, grassy areas, or areas dominated by European weeds, one will almost certainly find nothing but Lumbricidae. *Argilophilus garloughi*, *Toutellus toutellus*, *A. sierrae*, and a few other natives have been found to persist in disturbed areas such as grazed hillsides with oaks and in wheat fields, but this is usually (not always) in reduced numbers and in specialized microhabitats. Although *T. toutellus* and *A. sierrae* have been found to feed on the underside of aged cattle dung, this is an extremely unusual practice for this group. Further, the native taxa rarely travel over the surface as the Lumbricidae so commonly do. In consequence of the above, very few people, including biologists, ever see the native species.

Optimal Soil and Organic Matter Characteristics

In the extensive areas dominated by native forest, the Argilophilini are the predominant worms, and Lumbricidae are very rare, existing only in a few specialized habitats. Abundance of the natives can range from quite sparse (0.5 m^{-2}) in the Cascade Range to levels more nearly like those of agricultural soils (e.g., $30+ \text{ m}^{-2}$ at Castle Crags State Park, California).

Driloleirus macelfreshi, *D. wellsi*, and *D. cascadiensis*, all of which can reach 60 cm or more in length, can be found every 1–2 m along trails in favorable sites. Obviously, these worms can and do exert a dominating influence on soil structure and chemistry in much of the west. There are areas (e.g., under *Ceanothus* sp. on lower Table Rock, Jackson County, Oregon) where the entire A₁ horizon can be seen to be composed of the pelletlike castings of the local earthworms. On Vancouver Island, Graeme Spiers et al. (personal communication) found 40–50 large specimens per square meter of an undescribed *Arctiostrotus* sp. and observed that the acid, very deep (0.5–1.5 m) organic layer in virgin forests of this region was composed entirely of castings of this species.

The preferred habitats of the various species are quite diverse but fall into several groups. Members of the genus *Argilophilus* are largely soil feeders, living in the A₁ horizon of fine-textured soils and feeding indiscriminately on a mixture of soil and organic fragments. Most *Argilophilus* spp. are found in areas of mixed forest, including both hardwood and coniferous trees. This is a large genus, with many subgroupings, some species of which are litter feeders, but the rule will hold for most.

Most *Driloleirus* spp. make permanent burrows in fine-textured, compact, deep soils. They feed exclusively on organic fragments at or near the surface, including mosses, decaying conifer needles, bits of wood, grass seeds and stems, and an occasional dead insect. (A single undescribed species lives in and feeds on red clay soil.) Their burrows can be quite deep, having been traced down almost 5 m in Palouse soils near Pullman, Washington (Smith 1897). Several species will cast on the surface. Concentrations of these worms often occur where the water table is reachable but have not been found in waterlogged soil. Specimens of *D. macelfreshi* and *D. wellsi* kept in glass containers in the laboratory spent most of their time at the surface of an artificial water table (W. M. Fender, personal observation).

Arctiostrotus spp. live in concentrations of fairly raw organic matter, (i.e., upper litter layers of coniferous forest, soft rotting wood of old logs, in moss layers, and in well-aerated muck of cold seeps and small streams). Several species are specialists, while *Arctiostrotus perrieri*, which ranges from Coos Bay, Oregon, to the Queen Charlotte Islands and inland to the Cascade Range, takes advantage of all the foregoing habitats. These taxa are extremely intolerant of heat and will decompose quickly in a room that is comfortably warm to humans.

Species of *Toutellus* also live in organic matter, but they tend to be found in the lower organic layers (O₂) and into the upper mineral soil layers. One (undescribed) species is a true limicole and most can be found in or near aquatic situations, but more are not limited to such situations. *T. toutellus* is often found on dry slopes covered sparsely by *Quercus garryana*, the Oregon white oak, where they are found in the litter or organic-rich soils under the trees.

Chetodrilus will inhabit both litter and soil, and at least one species lives in well-rotted wet wood and in the mud of streams. These taxa are limited to within a few miles of the coast between Reedsport, Oregon, and Trinidad, California, and are probably dependent on the combination of high rainfall and moderate temperatures characteristic of that region. *Chetodrilus umbellulariae* is the most widespread species, being extremely opportunistic, and can be found in a wide variety of habitats [e.g., soil under redwoods, deep litter under *Lithocarpus* (tan oak), extremely acid litter on Blacklock soil (spodosol) under shore pine, or in rotting wood].

Most species of *Nephrallaxis* inhabit litter only, but unlike other litter inhabitants are found in the interior valleys of southwestern Oregon, although *N. davisii* and an undescribed species extend to the south Oregon coast and one, *N. blacki*, gets up to the central Willamette valley. One species, undescribed, from Lower Table Rock, near Medford, Oregon, was abundant in soil under *Ceanothus*, and the A₁ horizon consisted almost entirely of its castings. The soil between the shrubs, on the other hand, was nearly structureless. Another species was found within Oregon caves, but normally inhabits the litter of mixed conifer-hardwood forests.

Kincaidodrilus spp. are restricted to within a few kilometers of the coast in Washington and northwestern Oregon. Their ecology is poorly known but they seem to be primarily soil feeders and can stand a considerable amount of disturbance. An undescribed species has been found under grasses and herbs along a major highway and in a plowed field. Many of the known localities for *K. kincaidii* had been disturbed by logging or road building.

A common feature of native earthworms is for them to be found in higher numbers along trails and in other areas of compacted soil. Many of our best collections have been from old logging skid roads and within forest camps. Some species seem to have a reticulated distribution, determined largely by the game trails which are quite abundant in our forests.

Within the forested regions, there are certain kinds of sites which are much more likely than others to be inhabited by lumbricids to the exclusion of natives: streambanks and floodplains, especially if the associated soils are coarse-textured silts or sands; areas near roadsides, especially if dominated by hardwoods such as red alder (*Alnus rubra*) and with silty soils; campsites; open areas with blackberries or grasses, meadows; former pastureland regrown to forest (especially if with silty soil); and areas near fishing streams. Factors such as pH, calcium availability, and history of introduction also being important, not all of these areas will actually support lumbricids, but it is more likely that they will.

Serpentine Soils

In southwestern Oregon and northern California are large areas dominated by serpentinitic soils. These areas have a peculiar flora dominated by shrubs and are much more open than surrounding areas. The soils are rich

in clays and magnesium and often have high levels of toxic heavy metals (White 1971, Whittaker 1954). Native megascolecid earthworms (all undescribed species) are abundant in these soils but the Lumbricidae are absent. Interestingly, those local species are much more resistant than is normal to our technique of anesthetization with MgSO_4 .

Moisture

The lower limit of precipitation tolerated by argilophiline species appears to be about 15 in. (38 cm) annual precipitation. This is about the edge of moist forests in our area, although the range of *Driloleirus americanus* extends into treeless areas. While some argilophiline species are semi-aquatic, none seems to take advantage of moist situations in otherwise arid environments, such as do some Lumbricidae. The native taxa usually live in fine-textured soils, generally clays, clay loams, or silt loams, and those few species found in areas of sandy soil actually live in litter layers overlying or interbedded within the sand. Most species live in moderately acid soils (pH 6.5–4.5), but some are found in high abundance in organic soils of less than pH 3.0. Our only collections of native taxa from basic soil (8.0) were from serpentinitic clays. Soils inhabited by Argilophilini average lower in pH, finer in texture, and higher in woody (or otherwise hard to digest) organic matter than soils inhabited by Lumbricidae.

Preservation

Although it is possible to identify specimens that are poorly preserved, it is a difficult task. Also, we have found that the most valuable specimens and those easiest to study are those which have been relaxed prior to fixing. The following method has been developed over a period of nearly 40 years, by James A. Macnab and the authors and if carefully followed can yield excellent specimens with good color and excellent internal detail. It is a modification of a method used initially with marine invertebrates (Hedgpeth, personal communication).

This method involves four separate steps: anesthetization, killing, fixing and preservation.

1. After the worms have been rinsed (in cold water), place them in a MgSO_4 solution which contains 3–4 parts water to 1 part saturated MgSO_4 solution. It is generally best to start with a more dilute solution and add the saturated solution gradually. After a period of 30 minutes to 3 hours (usually 1 hour) the worms will be relaxed and unresponsive to mechanical stimulus, at which point they can be killed and fixed (but see note on serpentine soils above). If they become wrinkled, they must immediately be taken to the next stage before they decompose.

2. Dip the worms briefly (2–5 seconds) in Bouin's picro-formol, then lay them straight, extended but not stretched, on a sheet of paper for about 1 minute. This time is very approximate, but must be long enough for the tissues to be killed; otherwise, the longitudinal muscles will contract irreversibly in the next step. Bouin's picroformol is the only solution we have found which, while killing them, will still reliably leave the worms extended. Various methods that work well for Lumbricidae are unreliable with the Argilophilini. Immersion in hot water, for example, will cause some argilophiline worms to fall apart immediately. Some of the very large *Driloleirus* spp. can be killed in hot water, but the water must be hot enough to coagulate proteins. Contracted megascolecids are much more difficult to work with than lumbricids because they contract much more strongly. The internal organs end up lying on top of each other and segmental positions are obscured.

3. Put the worms in a V-shaped container, such as a dissecting tray elevated on one edge, and add enough Lavdowsky's solution (a mixture of formalin, alcohol, and acetic acid) to cover the specimens. At present, we are using a modified formula with half the acetic acid of the formula given by Guyer (1936). The worms will be stiff and ready to put in tubes in about half an hour but should be kept in the Lavdowsky's solution for at least several hours. Put the specimens in stoppered glass culture or test tubes and lay the tubes flat; the specimens can be folded to fit them in the tubes.

4. Replace the Lavdowsky's solution with 4% formaldehyde solution (9 parts water to 1 part commercial formalin) and afterward keep the tubes upright. If cork stoppers are used, care must be taken to ensure that the fluid, specimens, and labels do not touch the cork, or they will be blackened beyond use. The fluid should be replaced within a week and in any event should be replaced if it becomes cloudy, if the tubes are opened frequently, or after several years of storage. Care should also be taken that there is more volume of preservative than specimens. (It is astonishing how often this simple principle is ignored.)

Do not place unfixed earthworms directly into 70–80% alcohol and expect to get usable specimens. They become extremely flaccid and are of little or no scientific value. The internal organs dissolve to almost nothing recognizable, external features disappear, and all pigments are usually washed away. Formalin is essential for the fixation of delicate earthworm tissues. If there is no time to preserve them properly, worms can be placed directly in Lavdowsky's solution or Bouin's picro-formol and be usable (although badly contracted), but even then the fixing fluid should be replaced with 4% formaldehyde after several hours or overnight.

An efficient method for use during collecting trips is to lay the worms which have been dipped in Bouin's on a 3 by 5 in. file card and then slip the whole card, worms and all, into a small self-sealing polyethylene bag. Enough Lavdowsky's solution to cover the specimens when the bag is held

by the top is then poured directly into the bags, the air forced out, and the bag sealed. After several hours the fixative is strained out and replaced with 4% formaldehyde as above, the bags resealed, rolled up, and placed in glass-top canning jars, which are then filled with 4% formaldehyde. Many collections can thus be put into a small space and transported efficiently, not to mention the savings on tubes and chemicals. Collection data can be written directly on the cards, preferably in pencil or some resistant ink, and thus not get separated from the specimen.

Fixative and Preservation Solutions

Lavdowsky's Mixture (FAA) (Modified)

Water	40 parts
95% ethyl alcohol	50 parts
Formalin	10 parts
Acetic acid (glacial)	1 part

Bouin's Picro-formol

Picric acid, sat. aq. sol.	75 parts
Formalin	25 parts
Acetic acid (glacial)	5 parts

Note: Picric acid should never be allowed to become perfectly dry, as it then becomes a dangerous explosive. For this reason it is always sold with a sufficient moisture content. We recommend keeping the powder under water and using the resulting saturated solution. Rinse the cap of the container with water before attempting to open it so that no dry powder is left around the lip.

KEY TO THE MEGADRILE FAMILIES OF THE UNITED STATES*

- 1a Hearts 11 pairs, in xi–xxi; ovaries in xxiii; testes 10 pairs xii–xxi (large mud-dwelling worms of southern United States)
Lutodrilidae (*Lutodrilus multivesiculatus*)*
- 1b Hearts fewer, only anterior to xiv; ovaries in xiii; testes one to two pairs in x–xi **2**
- 2a An intestinal gizzard present in or behind segment xvii; calciferous gland intramural, consisting of longitudinal tubules within the esophagus wall, opening anteriorly; typhlosole present, involving all layers of gut wall
Lumbricidae
- 2b Gizzard not intestinal, if present; calciferous glands various, but not as above; typhlosole present or absent, if present then involving only inner gut wall and enclosing a vascular sinus **3**
- 3a With one or two (not more) pairs of “prostates” in or adjacent to the male pore

* Asterisks indicate species not yet reported from the western United States; included in this key for increased usefulness.

- segments, these prostates having a glandular, rough-textured ental portion and a basal duct portion with shining circular muscle **4**
- 3b** Prostates present or absent, but never as described above **5**
- 4a** Extramural calciferous glands present in ix and x; last hearts in segment xi. **Ocnerodrilidae**
- 4b** Calciferous glands various, but never extramural in ix and x only; last hearts in segment xii or xiii **Megascolecidae (s. lat.)*†**
- 5a** Prostates a pair in xvii, extending backward under the intestine, shining, covered with longitudinal (apex to base) muscle; female apparatus complex, ovaries in sacs connected to "spermathecae," which open into the oviduct; esophageal gizzard present; typhlosole absent . . . **Eudrilidae (*Eudrilus eugeniae*)***
- 5b** Prostates, if present, a long series of small glands associated with the ventral setae; ovaries, oviducts, and spermathecae all separate, not joined **6**
- 6a** Calciferous glands present, extramural in vii–ix; typhlosole present; gizzard present, esophageal **Glossoscolecidae (*Pontoscolex corethrurus*)***
- 6b** Calciferous glands absent; typhlosole absent; gizzard present or absent . . . **7**
- 7a** Gizzard absent **Sparganophilidae**
- 7b** Gizzard present, esophageal. **Komarekionidae (*Komarekiona eatoni*)***

Megascolecidae s. lat.

The family-level classification of the megascolecoid earthworms is in chaos. The western endemic taxa, as an example, cannot be satisfactorily fitted into the schemes of either Gates (1959), who recognizes three distinct families in this group, or Jamieson (1972), who places these same taxa into two subfamilies. Sims's (1980) treatment does not provide a place for the western endemics. For these reasons, we choose for the present to consider only an inclusive family Megascolecidae, which has well-defined limits, without subdivisions, rather than using subdivisions that are unnatural. Whereas according to the classifications of Gates (1959) and Sims (1980), the western natives would be placed in two separate families, Acanthodrilidae and Octochaetidae, they are a homogeneous group that is referable to a single tribe by our concepts. For this and other reasons we place them only in the inclusive family Megascolecidae. [For an overview of the dispute over family-level classifications in the megascolecoid earthworms, see Jamieson (1971), Gates (1959), and Sims (1980).]

KEY TO GENERA OF WESTERN MEGASCOLECIDAE‡

Due to time constraints and the presence of so many undescribed species in the western United States, no attempt will be made to key to the species level.

- 1a** Setae perichaetine (very many per segment); prostate gland branched, racemose **2**
- 1b** Setae lumbricine (eight per segment, in regular rows); prostate glands unbranched **3**
- 2a** Holonephric (one pair of nephridia per segment) ***Perionyx excavatus****
- 2b** Meronephric, nephridia a great many tiny twists on the peritoneum, giving it a

† See discussion under the family.

‡ Includes three genera not yet reported from the West.

Sims and Easton (1972) subdivided this unwieldy genus. Those interested in pursuing this problem should consult that reference as well as Gates (1972 and 1982).

- Dichogaster*

The species listed under this heading are a tightly knit group but include several recognizable genera, three of which (*Argilophilus*, *Kincaidodrius*, *Arctiostrotus*) have been described previously. Except for two *Argilophilus* species (*A. marmoratus*, *A. papillifer*), all the species in this group were originally described as *Plutellus* or *Megascolides*, which at the time were considered to be widespread genera with many species in Australia, New Zealand, Asia, and North America. *Argilophilus* Eisen,

1893 was synonymized with *Plutellus* by Michaelsen (1900). According to modern concepts, *Plutellus* and *Megascolides* are now each restricted to a few Australian species. Accordingly, Jamieson (1972) resurrected *Argilophilus* for the American *Plutellus* but did not formally transfer any of these species. Gates (1977b) formally transferred all of the described western *Plutellus* to *Argilophilus* except for *Plutellus* (= *Kincaidodrilus*) *kincaidu*, which has extramural calciferous glands and therefore did not fit his concept of *Argilophilus* (nor ours!), and *P. panulirus*, which was apparently overlooked. (In addition to the name changes, Gates gave brief "aids to the study of the genus" in the form of comments on the species, most of which, however, are either erroneous or misleading, due to his lack of experience in the group.) Two more plutelline genera have recently been described, *Kincaidodrilus* McKey-Fender, 1982 and *Arctiostrotus* McKey-Fender, 1982 (McKey-Fender and Fender 1982), but several remaining species do not belong in *Argilophilus* and new genera for these are described in this chapter.

- 1a Meronephric (with many pairs of nephridia in each segment)
Driloleirus, gen. nov.
- 1b Holonephric (with only a single pair of nephridia in each segment) 2
- 2a Intestine with dorsolateral caeca adnate to the anterior septa starting in region of xxiii–xxv *Toutellus*, gen. nov.
- 2b Intestine without such caeca 3
- 3a Prostomium tanylobic with nephropores of segment ii at or near ends of prostomial grooves; last hearts in xiii, nephrostomes functional through length of body. *Arctiostrotus*
- 3b Nephropores of segment 2 not at ends of prostomial grooves; if prostomium tanylobic, then last hearts in xii, nephrostomes reduced to small stalked clumps of cells in all but rectal region 4
- 4a Commissure of v on posterior gizzard, septum 5/6 fairly well developed; gizzard entirely in segment v 5
- 4b Commissure of vi on posterior gizzard, of v on anterior gizzard margin, septum 5/6 weak, closely investing gizzard or gizzard at least partly in segment vi or posterior 7
- 5a Calciferous region with extramural calciferous glands in all or some of xiv–xvii, at least dorsolateral sacculations (pouches), at most large paired glands with narrow openings; longitudinal lamellae are continuous into these sacculations. *Kincaidodrilus*
- 5b Calciferous region with or without enlargements but not segmental paired glands. 6
- 6a Intestine with mV cecum near typhlosolar origin.
Macnabodrilus gen. nov.
- 6b Intestine without caeca of any kind; covering of anterior intestine a white, pearly layer, removable in thin sheets; dorsointestinal vessels large, pulsating in life. *Drilochaera*
- 7a Spermathecal pores obvious, one to four pairs; prostate duct well developed, sometimes huge. 8
- 7b Spermathecal pores small, although often associated with obvious glandular papillae; prostate duct small; calciferous lamellae all longitudinal or a mixture of longitudinal and transverse; spermathecae always two pairs
Argilophilus
- 8a Prostate ducts very long, strong, extending most of height of worm; calciferous lamellae all transverse; spermathecae two to four pairs; axis of typhlosole

- evenly corrugated vertically, like a washboard; typhlosole often T-shaped in cross section *Chetcodrilus*, gen. nov.
- 8b Prostate ducts only somewhat less strong; calciferous lamellae longitudinal; typhlosole simple; spermathecae one to two pairs. . . . *Nephralaxis* gen. nov.

***Driloleirus* gen. nov.**

Type Species: *Megascolides americanus* Smith, 1897

Other Included Species: *Megascolides wellsii* Altman 1936, *Megascolides macelfreshi* Smith 1937, *Megascolides cascadenis* Smith 1937, *Megascolides ciseni* Smith 1937, *Megascolides michaelsoni* Smith 1937, and three or more undescribed species

Diagnosis: Anterior and posterior ends bulbous, anterior septa nested. Unpigmented. Prostomium in juveniles epilobous with parallel grooves nearly to one-half, with cross groove near the anterior of segment, wide anteriorly. In older worms this portion appearing prolobous or short epilobous closed behind or tanylobous. Clitellum saddle $\frac{1}{2}$ xii– $\frac{1}{2}$ xix(xxiii) varying specifically. Dorsal pores not conspicuous, present in all postclitellar segments, posterior one to five pores enlarged. Setae ventral, widely paired. Metonephric throughout. Nephridia behind gizzard separate, exoic, in regular longitudinal rows, a single transverse series per segment; nearly constant in number per segment behind prostates. Median nephridia possessing (functionless) funnels except in some ante-prostatic segments; enlarged in caudal bulb. Buccal enteronephry in one species. Genital markings intersegmental. Spermathecae paired in viii and ix or in ix. Pores conspicuous; duct short, thick-walled with one or more intramural to sessile diverticula; duct expanded ectally (vaginal?). Prostate gland long but tightly coiled, rarely entering adjacent segments, duct short. Penial setae stout, sculptured, reserve setae often fascicled. Peniseta and male pores not united, on paired, round glandular porophores. Gizzard in v, commissures of v on posterior third of gizzard. Calciferous region dilated to sacculated; some lamellae transverse midsegmentally (varying specifically). Intestinal origin xvii to xix, usually xviii, preintestinal constriction two segments. Typhlosole always present, a simple lamellar ridge or with free edge once or more bifurcate. Ventral ciliated intestinal groove absent (at most sometimes rudimentary?) Last hearts xiii. Vascular systems with posterior longitudinal intersegmental connections of both afferent and efferent systems present but always on lateral parietes, never midventral. Posterior lateroparietal vessels having branches both of subesophageal vessels and directly to esophagus. Lymph glands inconspicuous, not enveloping dorsal vessel (a characteristic of *Megascolides* s. str.).

Range: West of Cascade Range from Cowlitz and Skamania counties in Washington, south to Lane County, Oregon. East of Cascade Range in vicinity of Pullman and Clarkston, Washington; Moscow, Idaho; and Ellensburg, Washington.

***Arctiostrotus* McKey-Fender, 1982**

Type Species: *Plutellus perrieri* Benham, 1892

Other Included Species: *Plutellus altmani* Gates, 1942, and seven undescribed species

Diagnosis: Pigmented or unpigmented, pigment in muscle layers. Prostomium tanylobic. Clitellum xiii–xviii, annular. Dorsal pores lacking except a few in caudal bulb. Nephropores alternating at two levels, first pair at or near ends of prostomial grooves. Holonephric exonephridia, vesiculate (vesicles may be inconspicuous), terminal ducts of one or more successive anterior segments confluent bilaterally in some species. Genital markings segmental, intersegmental, or a combination (rarely absent). All genital pores small, superficial. Spermatheca three to five pairs, last pair in ix. Prostates with slender ducts, confined to xviii; prostate pores and peniseta pores united. Penial setae weak, small, but present. Moderate gizzard in v, v and vi,

or vi. Commissures of v on anterior of gizzard, of vi on posterior. Esophagus simple, calciferous lamellae low, predominantly longitudinal, or partly transverse, short. Intestinal origin xvii, without ceca or ventral ciliated groove. Typhlosole present, a simple lamella or nearly obsolete, reduced to a dorsal longitudinal vein. Last hearts xiii, dorsal part of hearts of x–xiii long. Posterior lateroparietal trunks join bifurcation of continuous subesophageal vessels in xiii. Anterior lateroparietal trunks originate from small vessels below ventral valves of commissures of vii, viii, and especially ix, slender. Both lateroparietals extend to posterior end of body. Vascularization of intestinal wall quadrangular with dorsointestinals visible as slender, paired vessels perpendicular in lateral view. Musculature of body wall thicker ventrally, ventral setae large, those of spermathecal segments (vi–ix) very large. Dorsal interval narrow to wide, $DD < \frac{1}{3}C$ to $\frac{1}{2}C$ (specific variation).

Range: Islands of western British Columbia, south along the coast and in the Puget Trough of Washington; Oregon west of the Cascade Range summits south to Coos Bay, exclusive of the Willamette Valley floor; and in the mountains of central Idaho (Clearwater and Latah counties).

***Macnabodrilus* gen. nov.**

Type Species: *Plutellus macnabi* McKey-Fender, 1957

Other Included Species: *Plutellus hopsonae* McKey-Fender, 1970

Diagnosis: Unpigmented. Prostomium epilobic. Clitellum saddle xiii–xviii. Dorsal pores large, beginning anterior to clitellum. Holonephric, exoic, heteropore, avesculate. Genital markings intersegmental. Quadrithecal in viii and ix. Seminal chambers anteromedially intramural in duct. Penial setae stout (may be fascicled), sculptured with rows of spines. Male and penisetal pores close or united. Gizzard in v, commissures of v on posterior one-third of gizzard. Calciferous region broad, constricted septally, some lamellae transverse. No extramural calciferous glands. Typhlosole lamellar or T-shaped (specific variation), double ventral esophageal typhlosole. Intestine beginning xviii. Intestinal groove distinct, wall uniformly thick throughout, a midventral cecum opposite beginning of typhlosole, involving all layers of intestinal wall. Last hearts xii. Anterior lateroparietal trunks from ventral part of hearts of ix. Posterior lateroparietal trunks join paired adnate subesophageal vessels in xiii. Both lateroparietal trunks extend to end of body. Vascularization of intestinal wall a finely quadrangular sinus; dorsointestinal veins perpendicular in lateral view. Dorsal interval very wide, $DD > \frac{1}{2}C$.

Range: Washington south of Puget Sound in Puget Trough and Wind River area; in Oregon just south of the Columbia River in Clatskanie area, Columbia County.

***Kincaidodrilus* McKey-Fender, 1982**

Type Species: *Plutellus kincaidii* Altman, 1936

Diagnosis: Unpigmented. Prostomium small, epilobic closed behind or nearly prolobous. Clitellum saddle, xiii–xviii. Dorsal pores large, beginning anterior to clitellum. Nephropores very inconspicuous, alternating at two distinct levels. Holonephric exonephridia, avesculate; postclitellar tubules not parietal, on a mesentery. Genital markings intersegmental. Diagonal glandular bars form male field. Bithecal or quadrithecal in ix or viii and ix (specific variation). Pores small slits with tumid lips; ample ampulla and stout duct with multilocular sessile diverticulum anteriorly or anterolaterally. Prostates confined to xviii, very long, bulging septa, duct moderate. Penial setae very long and fine, capillary; sculptured with fine transverse streaks. Male and penisetal pores united on conical porophores. A strong rounded gizzard in v, commissures of v on posterior one-third of gizzard. Esophagus complex, in region of (xiii)xiv–xvii with dorsal paired pouches with

strong longitudinal lamellae, ranging from simple outpocketings to basally constricted sessile calciferous glands with narrow openings into esophageal lumen. Intestine beginning xviii or xix, without ceca and with simple shallow intestinal groove. Typhlosole present, very large, T-shaped in cross section. Last hearts xii. Anterior extrasophageal trunks form slender, paired subesophageals in vii or viii to xi and xiii (not found in xii). Posterior lateroparietal trunk joins esophagus directly in xiii. Anterior (ventral) lateroparietals from ventral part of commissures of ix, conspicuous anterior to clitellum, but posteriorly traceable only as slender connectives in BC between circumferential vessels on parietes. Most vascular elements of intestine wall vertical. Musculature of body wall not divided. Setae regular, paired, none especially enlarged. Dorsal interval wide, $DD > \frac{1}{3}C$.

Range: Washington, northwest Olympic Peninsula (Clallam, Jefferson, Gray's Harbor, and Mason counties) south along the coast in Willapa Bay area and Pacific County, Oregon in the Columbia River lowland forest (Clatsop County) near Astoria and along coast as far south as Cape Meares (central Tillamook County).

***Toutellus* gen. nov.**

Type Species: *Plutellus toutellus* Altman, 1936

Other Included Species: *Plutellus oregonensis* Smith, 1937, *Plutellus oregonensis* *sicifiae* Smith, 1937, *Plutellus hyonides* Macnab and McKey-Fender, 1959, *Plutellus adaeus* Macnab and McKey-Fender, 1959, and (at least?) four undescribed species

Diagnosis: Bulbous anteriorly, slender posteriorly, phallic in contraction. Usually, unpigmented or immatures with red epidermal alcohol-soluble chromophores (specific variation). Epilobic open behind. Clitellum annular xiii–xviii ($\frac{1}{2}$ xix dorsally). Dorsal pores present behind clitellum (uncommonly beginning 14/15). Holonephric exonephridia, avesculate; pores alternating irregularly, very inconspicuous. Genital markings intersegmental. Quadrithecal ducts stout, seminal chambers intramural in anterior wall of duct, bulging duct walls. Prostates confined to xviii, moderately short to long, ducts moderately stout. Penial setae strong, curved, ornamented with rows of teeth or scales. Male and penisetal pores separate on low, raised porophores. Strong gizzard in v, v and vi, or vi. Commissures of v on anterior of gizzard, of vi on posterior or farther forward. Calciferous lamellae longitudinal, low to high, continuous in (xiv)xv–xvi. Intestine beginning xviii (rarely xvii?), with ceca and ventral intestinal groove. Ceca paired dorsolaterally and/or laterally on intestine, anterior several pairs adnate to and supported by anterior septa of their segments; saccate to digitate, a series in region of xxii to 1x. Typhlosole lamellar to branched T-shape in cross section. Last hearts xii or xiii (specific or individual variation). Anterior (ventral) lateroparietal trunks originate below ventral valve of commissures of ix. Posterior (dorsal) lateroparietals enter esophagus in xiii. Subesophageals not continuous. Both lateroparietals extend to rear of body. Epidermal capillaries longitudinal. Musculature of body wall continuous, thickness nearly uniform dorsally and ventrally. Setae regular. None especially enlarged. Widely paired to separate. Dorsal interval wide $DD > \frac{1}{3}C$.

Range: British Columbia, Vancouver Island; Washington west of the Cascade Range and in the central Puget Trough, south in Oregon west of the Cascade Summits, in the Cascade Range and central valleys to the Douglas–Jackson county line, and along the coast to southernmost Curry County. Not yet known from the Washington coast or California. Ranging in elevation from sea level to at least 1280 m (4200 ft).

***Chetcodrilus* gen. nov.**

Type Species: *Plutellus umbellariae* Macnab and McKey-Fender, 1958

Other Included Species: *Plutellus fenderi* Macnab and McKey-Fender, 1958, *Plutellus exutus* Macnab and McKey-Fender, 1958 and two(?) undescribed species

Diagnosis: Unpigmented. Epilobic. Clitellum xiii–xviii, annular over several anterior segments. Dorsal pores present behind clitellum. Nephropores modified heteropore. Holonephric exonephridia, avesculate. Genital markings intersegmental. Quadrithecal; (quadrithecal to octothecal in the type species); spermathecal duct ectally shining, strengthened with circular muscles. Pores small, distinct round pits, in adults closed with mucous plugs; seminal chambers intramural, bulging duct, or sessile on duct. Prostates large, drawn back into xix, gland plicate, ducts strongly muscular. Penial setae spined. Male and penisetal follicles united or nearly so, even in species with strong penial setae. Gizzard in v and vi or vi, commissures of v on anterior of gizzard. Calciferous lamellae simple, rippled, transverse, sharply defined posteriorly, esophagus not enlarged, ventral esophageal typhlosole double, extending posteriorly into first intestinal segment beyond other lamellae of preintestinal constriction. Intestinal origin xvii. No intestinal ceca. Distinct ventral intestinal groove opposite typhlosole. Typhlosole lamellar (with square or grooved face) to broadly T-shaped. Axis with many strong vertical veins. Last hearts xii or xiii. Posterior lateroparietals join bifurcations of continuous paired subesophageal trunks in xiii. Vascularization of intestine a rectangular sinus grid, neither anterior nor posterior dorsointestinals especially prominent. Musculature of ventrum slightly stronger. Ventral pairs of ambulatory setae slightly enlarged. Dorsal interval $DD = \frac{1}{3}$ to $\frac{1}{2}C$ (specific variation).

Range: Limited to coastal and near coastal areas from Coos County, Oregon, south to Patrick's Point near Trinidad, Humboldt County, California.

Nephrallaxis gen. nov.

Type Species: *Plutellus davis* Macnab and McKey-Fender, 1953

Other Included Species: *Plutellus blacki* Macnab and McKey-Fender, 1953, and at least seven undescribed species

Diagnosis: Mostly small rather stout worms. Unpigmented or with red epidermal chromophores (one species). Prostomium long-epilobic to tanylobic. Clitellum annular, xiii–xviii. Dorsal pores present beginning 12/13 (usually evident only behind clitellum). Heteropore. Holonephric exonephridia, avesculate. Postclitellar tubules compactly arranged, low on parietes (always?). Genital markings segmental or intersegmental or a combination, or absent. Bithecal in viii or ix or (one species) quadrithecal in viii and ix, with expanded pores in 7/8 or 8/9 or 7/8 and 8/9. Seminal chambers intramural, sessile on duct, or sperm contained in duct lumen. Pores of mature individuals closed by mucous plugs. Prostates with strong to very strong ducts entrant into xix. Lateral musculature vicinity of prostates very strong. Penial setae strong, curved; ornamented with rows or groups of sharp spines. Prostate and penisetal pores separate. Gizzard vi or vi and vii. Commissures of v on anterior of gizzard, of vi on posterior of gizzard or farther forward. Esophagus tubular, calciferous lamellae low, discontinuous, mainly longitudinal, a few scattered transverse folds between main lamellae. Intestinal origin xvii; lacking ceca, ventral groove simple. Typhlosole lamellar with rounded free edge containing a sinus. Preintestinal constriction short (parts of two segments). Last hearts xii. Hearts long above valves. Posterior lateroparietal trunks join bifurcation of continuous paired subesophageals in xiii. Anterior lateroparietals from below ventral valve of commissures of ix. Both continuous to end of body. Vascularization of intestine wall rectangular, anterior dorsointestinals visible. Musculature of body wall thicker ventrally. Ventral setae slightly enlarged. Interval $DD < \frac{1}{3}C$ (always?). Setae regular, separate.

Range: Eola Hills (southern Yamhill and Polk counties), Salem (Marion County) south through Douglas and Jackson counties, Oregon, into northern California, Smith River (Del Norte County) north along the Oregon coast and Coos Bay in Curry and Coos counties and in western Douglas and Lane counties.

Drilocheira gen. nov.

Type Species: *Plutellus chenowithensis* McKey-Fender, 1970

Other Included Species: three undescribed species

Diagnosis: Slender worms with thin body wall. Unpigmented. Broadly epilobic. Clitellum pale, saddle (xii)xiii–(lxviii)xviii. Dorsal pores visible behind clitellum, may be present in clitellum, but obscured; last one or two enlarged. Holonephric, exoic, avesciculate. Nephropores irregular, inconspicuous. Genital markings intersegmental, visible internally through the body wall. Quadrithecal in xiii and ix; pores small. Seminal chambers intramural or forming extramural lateral, dorsolateral or paired median and lateral, sessile or short-stalked diverticula. Prostate gland length moderate, slightly flattened, ducts slender. Penial setae moderately stout to very slender, with toothed ornament, curved at least proximally (rarely absent?). One or three pores on each male porophore (correlated with degree of reduction of penial setae). Gizzard v, commissures of v on or behind middle of gizzard. Esophagus nearly cylindrical or very slightly broadened, not segmentally enlarged. Calciferous lamellae longitudinally oriented short ridges, fine longitudinal ridges or a combination, in (xiii)xiv–xvi (or in homologous segments preceding the preintestinal constriction and valve), moderate to high with tendency toward fusion medially. Flat or double ventral esophageal typhlosome extending into first intestinal segment. Intestine begins xvi, xvii, or xviii (specific variation). Pretyphlosolar region of intestine short, involving only one or two segments. Typhlosome lamellar to inverted T-shape in cross section (specific variation). Intestinal ceca absent. Ventral intestinal groove wide, shallow, flanked by low ciliated ridges. Last hearts xii. Dorsal vessel behind hearts broad, in anteriormost (two or three) intestinal segments very broad; dorso-intestinals in these segments also widened near dorsal vessel; naked dorsally and with heavy chloragogen laterally, forming a prominently pulsing organ in life, a crudely stellate pattern in the preserved state. Each posterior lateroparietal joining a bifurcation of the continuous paired subesophageals in xiii. Typhlosolar region of intestine, including dorsal vessel and dorso-intestinals, covered by a distinct, glistening (white to yellow) pearly layer closely investing and masking structures beneath. This is distinct from the chloragogen and covers it. Typical chloragogen mostly on esophagus and aggregated along dorsal vessel. Vascularization of intestinal wall longitudinal. Musculature not divided into separate bands, narrowly interrupted at setae. Dorsal setal interval moderate to wide, $DD = \frac{2}{5}$ to $\frac{3}{5}C$ (specific variation).

Range: The type species is from the Dalles area (east of the Cascade Range). Other representatives are from southwestern Washington south along the coast and in the Coast Range to Lane County, and in the Willamette Valley.

Argilophilus Eisen, 1893

Type Species: *Argilophilus marmoratus* Eisen, 1893

Other Included Species: *Argilophilus papillifer* Eisen, 1893, *Argilophilus collinus* Eisen, 1900, *Plutellus sierrae* Michaelsen, 1921, *Plutellus garloughi* Smith, 1937, *Plutellus panulirus* Macnab and McKey-Fender, 1959, *Plutellus hammondi* McKey-Fender, 1970 and at least 30(?) undescribed species

Diagnosis: Mostly slender worms. Unpigmented. Epilobic. Clitellum saddle or indefinitely or distinctly annular (xii)xiii–xvii. Dorsal pores present, sometimes very small. Nephridia holoic, exoic, avesciculate. Pores irregularly alternating with tendency in some species to form series in the same line. Genital markings intersegmental. Quadrithecal; spermathecal diverticula distinct, multilocular on lateral, anterior, or median face of duct, intramural or absent (then sperm received in ampulla). Pores small, though distinguishable. Prostate ducts weak in relation to glandular portion. Penial setae various. Male and penisetal pores separate or

united. Gizzard in v, v and vi, or vi. Commissures of v anterior on gizzard, of vi on posterior. Calciferous region not expanded, lamellae essentially longitudinal. Intestinal origin xvi–xviii (specific variation). Typhlosole distinct, lamellar to T-shaped (specific variation). Dorsolateral intestinal ceca if present shallow, not involving septa. Several species have a midventral cecum involving all layers of intestine wall, near origin of typhlosole. Midventral intestinal groove distinct, often broad, in one of the groups often with thin floor. Last hearts xii or xiii. Parietal trunks various; posterior lateroparietals join a bifurcation of continuous subesophageals, enter esophagus directly, or send branches both entering esophagus and joining subesophageals (specific and group variation). Vascularization of gut wall longitudinal, may be diagonal (group variation?). Musculature various. Setal intervals various. This is an extremely variable genus containing some groups that may be of generic or at least of subgeneric status.

Range: In Oregon throughout area west of Cascade Range, except extreme northwest coast and mid to high elevation in the Cascade Range. They have been found in two areas of the Ochoco and Blue mountains of eastern Oregon. In California they are known from as far south as Tulare County.

Described Species

- Driloleirus americanus* (Smith, 1897) comb. nov.
Driloleirus wellsi (Altman, 1936) comb. nov.
Driloleirus macelfreshi (Smith, 1937) comb. nov.
Driloleirus cascadenis (Smith, 1937) comb. nov.
Driloleirus eiseni (Smith, 1937) comb. nov.
Driloleirus michaelsoni (Smith, 1937) comb. nov.
Arctiostrotus perrieri (Benham, 1892) McKey-Fender and Fender, 1982
Arctiostrotus altmani (Gates, 1942) McKey-Fender and Fender, 1982
Macnabodrilus macnabi (McKey-Fender, 1957) comb. nov.
Macnabodrilus hopsonae (McKey-Fender, 1970) comb. nov.
Kincaidodrilus kincaidii (Altman, 1936) McKey-Fender, 1982
Toutellus toutellus (Altman, 1936) comb. nov.
Toutellus oregonensis (Smith, 1937) comb. nov.
Toutellus hyoiedes (Macnab and McKey-Fender, 1959) comb. nov.
Toutellus adocus (Macnab and McKey-Fender, 1959) comb. nov.
Chetcodrilus umbellulariae (Macnab and McKey-Fender, 1958) comb. nov.
Chetcodrilus fenderi (Macnab and McKey-Fender, 1958) comb. nov.
Chetcodrilus exutus (Macnab and McKey-Fender, 1958) comb. nov.
Nephrallaxis davisii (Macnab and McKey-Fender, 1953) comb. nov.
Nephrallaxis blacki (Macnab and McKey-Fender, 1953) comb. nov.
Drilochaera chenowithensis (McKey-Fender, 1970) comb. nov.
Argilophilus marmoratus Eisen, 1893
Argilophilus papillifer Eisen, 1893
Argilophilus collinus Eisen, 1900
Argilophilus sierrae (Michaelson, 1921) Gates, 1977
Argilophilus garloughi (Smith, 1937) Gates, 1977
Argilophilus panulirus (Macnab and McKey-Fender, 1959) comb. nov.
Argilophilus hammondi (McKey-Fender, 1970) Gates, 1977

For detailed discussion of the species see the references by Altman (1936), Eisen (1894, 1896), Gates (1942, 1962), Macnab and McKey-Fender (1947–1960), McKey-Fender (1957–1982), McKey-Fender and Fender (1982), and Smith (1897, 1937).

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